Seasonal and interannual evolutions of biogenic silica standing stock and production at the KERFIX time-series station off the Kerguelen Islands

by

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ABSTRACT. - The biogeochemical cycle of silicon was studied at the Kerguelen Fixed Station (KERFIX) between 1992 and 1994. The timeseries shows a seasonal use of the stock of silicic acid decoupled from that of nitrate. Thus, silicon probably plays an important role in limiting the primary production of diatoms in that area, characteristic of the permanently open ocean zone. Despite this, given their very low growth rates, the dominant diatoms are strongly silicified. The results of KERFIX are compared with more recent KEOPS (Kerguelen Ocean and Plateau compared Study) results and provide a complement to KEOPS in terms of understanding interannual and seasonal variability.

RÉSUMÉ. - Évolutions saisonnière et annuelle de la production et du stock de silice biogénique à la station KERFIX au large des îles Kerguelen.

Le cycle biogéochimique du silicium a été étudié à la station KERFIX entre 1992 et 1994. L'évolution temporelle montre une utilisation saisonnière du stock d'acide silicique découplée de celle du nitrate. De ce fait le silicium joue vraisemblablement un rôle important de limitation de la production primaire des diatomées. Malgré cela, compte tenu de taux de croissance très faibles, les diatomées dominantes sont très silicifiées. Les résultats de KERFIX sont comparés aux résultats plus récents de KEOPS et apportent un complément en termes de variabilité saisonnière et annuelle.

Key words. - Silicon cycle - Biogenic silica - Production - Diatoms - Si/N ratios.

Diatoms play a major role in the control of the biological pump of CO_2 of the World Ocean (Nelson *et al*., 1995; Tréguer *et al*., 1995). Both at present and in the past (e.g., Abelmann *et al*., 2006; Armand *et al*., 2008a, 2008b), these siliceous microalgae are known to significantly contribute to the primary and export production of the silicic-acid rich waters of the Southern Ocean. Among the subsystems of the Southern Ocean, the permanently open ocean zone (POOZ) represents a vast high nutrient, low chlorophyll (HNLC) area, whose bottom sediments are characterized by the world's largest sedimentary deposits of biogenic silica. In order to document the dynamics of planktonic development and biogeochemical cycles, a research program was conducted between 1990 and 1995 at a time-series station located in the POOZ near Kerguelen Islands, in reasonable proximity to the scientific base of Port-aux-Français to allow the use of light vessels to study the temporal variability of the ecosystem (Jeandel *et al*., 1998). The physical structure of the surface waters was characterized by low temperatures (1.6-4.3°C) and salinity range from 33.79 and 33.93, typical of Antarctic surface water (AASW), with a clear seasonal cycle marked by the shift from a stratified system of 100-150 m depth thermocline in summer, up to 300 m depth towards the winter in a homogeneous water column (Jeandel *et al*., 1998). This seasonal change in the physical environment is reflected in the development of a moderate plankton bloom (at most 87 mg chlorophyll *a* m^{-2}, Jeandel *et al*., 1998) which starts between September and December and is accompanied by a decrease of silicic acid (down to < 9 μM H_4SiO_4) that appears to play a major role in limiting siliceous phytoplankton production (Pondaven *et al*., 1998). In the following study, we aim to address two issues: the variability of the biogenic silica stocks and the silica production in the surface waters of the POOZ near Kerguelen, and the factors that control the availability of H_4SiO_4 for diatoms in the course of the seasonal cycle.

MATERIAL AND METHODS

From January 1990 to March 1995 surface waters (0-300 m) were sampled at KERFIX, located at 50°40' S, 68°25' E, 60 miles southwest of the Kerguelen Islands (Fig. 1). Water samples from the surface and/or wind mixed layer were taken by hydrological casts from the NO *La Curieuse* (IPEV). The physical, chemical and biological parameters were measured at the Kerguelen laboratory. Data were taken from the PROOF/INSU (Processus biogéochi-

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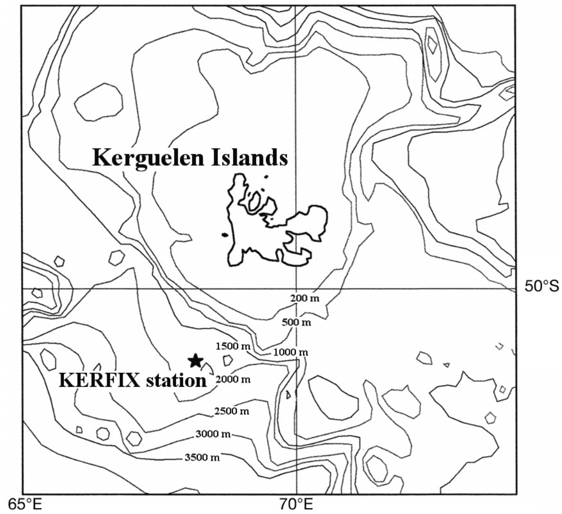

Figure 1. - Map of the study area: geographical location of the KERFIX station from January 1990 to March 1995.

mique dans l'océan et flux/Institut National des Sciences de l'Univers) database (http://www.obs-vlfr.fr/cd_rom_dmtt/kfx_main.htm). We have restricted data analyses for the first 300 m of the water column in this study. Nutrient analyses are available for the period between 10 June 1991 and 20 March 1995 but we have restricted the nutrient data analysis to the years 1992 to 1994 of the program, i.e., the period when a coherent time-series was obtained simultaneously with data on biogenic silica stocks and production.

For biogenic silica, two litres of sea water were collected at the sampling depth, and immediately transferred into two 1-L polycarbonate flasks, and brought back to the Kerguelen laboratory for treatment. At initial time (t_0) one 1-L volume was filtered onto a 0.6 μM polycarbonate membrane, for biogenic silica (BSi) determination at the Brest laboratory, following Ragueneau and Tréguer (1994); the silicic acid concentration of the filtrate was measured on a spectrophotometer according to the manual method of Mullin and Riley (1955). The second 1-L volume was enriched (~10% of initial H_4SiO_4 concentration) with an H_4SiO_4 tracer solution using the stable isotope ^{30}Si, and placed into an incubator cooled by running sea-surface water directly pumped from the Kerguelen harbour. After 24-hr incubation (t_f) this second sample was filtered onto a 0.6 μM polycarbonate membrane, for biogenic silica production (ϱSi) determination. The biogenic silica production was determined according to Corvaisier *et al*. (2005). A THQ-Finnigan thermal ionization mass spectrometer was used to measure the SiO_2 peaks at mass 60 (^{28}Si), 61(^{29}Si), and 62(^{30}Si) with determination of isotopic ratios at ± 1% precision. Specific rate of biogenic silica production (V_{PSi} (d^{-1})) was calculated from $^{30}A_f$ (^{30}Si enrichment in the particulate silica after incubation), relatively to $^{30}A_i$ (^{30}Si abundance in enriched seawater) corrected from ^{30}Si natural abundance: $V_{PSi} = (^{30}Af - ^{30}An) / (^{30}Ai - ^{30}An) \cdot \Delta t$; where Δt is the incubation time. Absolute rate of biogenic silica gross production was obtained through the formula: $\varrho Si(\text{mmol m}^{-3}\text{d}^{-1}) = V_{PSi} \times BSi$, where BSi refers to the total biogenic silica concentration (i.e., belonging to living diatoms and detritus material).

RESULTS

In the 0-300 m (AASW) layer, nutrient concentrations (Fig. 2) were typically high for nitrate+nitrite (NO_3+NO_2), never dropping to the limiting value for phytoplankton growth. Concentrations of NO_3+NO_2 ranged from 23.0 μM for the lowest summer value to 28.2 μM for the highest winter value. Ammonium (data not shown) was usually undetectable during winter but could increase up to 0.7 μM during summer, again a typical feature of AASW (Jacques, 1991). Concentrations of H_4SiO_4 reached up to 20.6 μM during winter. Although H_4SiO_4 was never depleted, it significantly decreased during summer, at values typically reported to limit Antarctic diatoms (down to 5.4 μM). During the study period biogenic silica and phytoplankton biomass varied seasonally, usually in phase. Phytoplankton biomass of the surface waters was low during winter (down to 0.09 mg m^{-3}) and increased during the bloom periods (up to 1.15 mg m^{-3}). In the same way biogenic silica low values were found during winter (minimum value of 0.11 μmol L^{-1}) while the high values coincided with blooms (maximum value of 5.3 μMol L^{-1}). It was notable that during summer

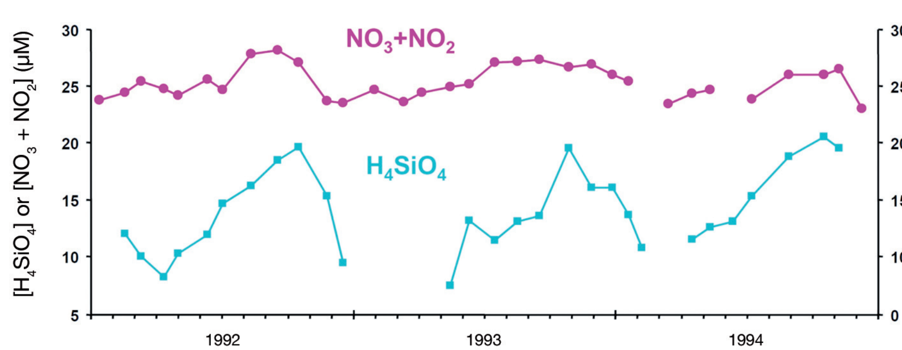

Figure 2. - Evolution of the concentrations of nitrate + nitrite (NO_3+NO_2) and silicic acid (H_4SiO_4) in the surface waters at the KERFIX station from 1992-1994.

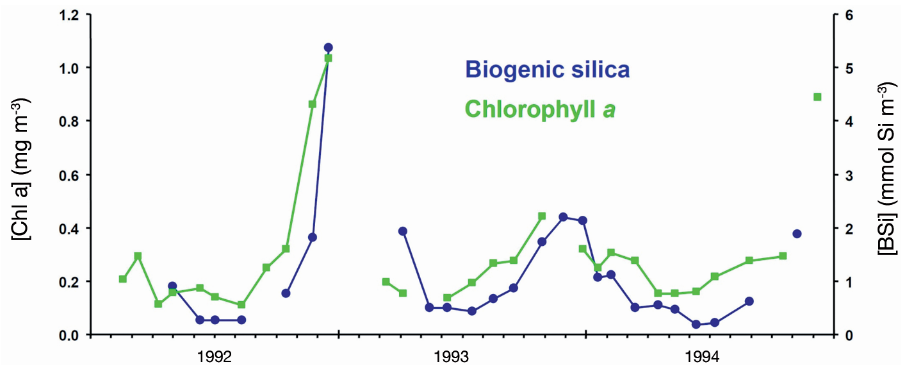

Figure 3. - Joint evolution of the concentrations of chlorophyll *a* (Chl *a*) and biogenic silica (BSi) in the surface waters at the station KERFIX from 1992-1994.

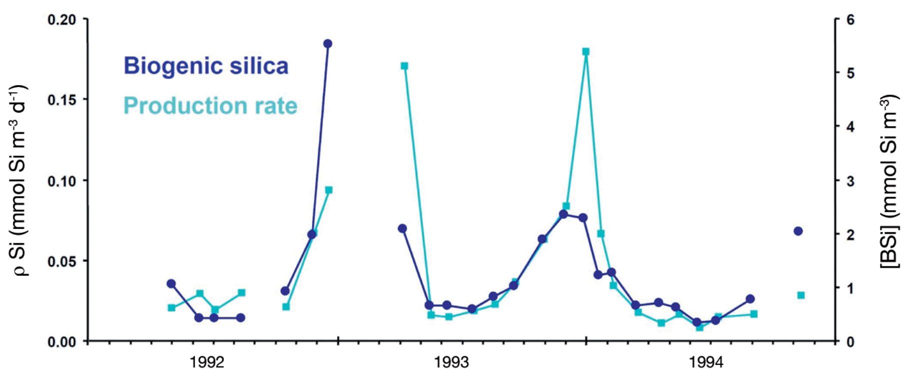

Figure 4. - Joint evolution of the concentrations (BSi) and the production rate (ϱSi) of biogenic silica chlorophyll *a* (Chl *a*) in the surface waters at the KERFIX station from 1992-1994.

1993-1994 both biogenic silica and chlorophyll *a* concentrations peaked at lower values compared to summer 1992-1993. Moreover, the evolution of biogenic silica production was parallel to that of BSi, but the asymmetry between the two blooms was not observed; ϱSi values were thus of the same order of magnitude in 1992-1993 as well as in 1993-1994 spring developments (~0.175 mmol Si m^{-3} d^{-1}).

DISCUSSION

The data obtained between 1992 and 1994 KERFIX can be compared to those obtained more recently (2005) during the *KEOPS* cruise (Blain *et al*., 2007). During the spring-summer period in KERFIX, when chlorophyll *a* levels at the surface were > 1 mgm^{-3}, V_{PSi} remained low averaging 0.02 d^{-1} in October-December 1992 and 0.05 d^{-1} in October 1993-February 1994. Interestingly, during the *KEOPS* cruise, east of the Kerguelen islands, comparable values were measured in the euphotic zone (Mosseri *et al*., 2008), both for the HNLC stations (0.06 ± 0.02 d^{-1}), and for the naturally iron-enriched stations (0.04 ± 0.04 d^{-1}). Correspondingly, ϱSi averaged 0.05 mmol m^{-3}d^{-1} in October-December 1992 and 0.08 mmol m^{-3}d^{-1} in October 1993-February 1994, which is comparable and even lower than the mean rate (0.20 ± 0.10 mmol m^{-3}d^{-1}) measured in the euphotic zone during *KEOPS* in January-February 2005 at the typical HNLC reference station (Mosseri *et al*., 2008). Another comparison can be made regarding the stoichiometric production ratios ΔSi/ΔN. Because of experimental problems, nitrogen production data of the KERFIX program are not available but the ΔSi/ΔN ratio, calculated as the ratio of the difference between austral summer and winter surface concentrations of H_4SiO_4 and NO_3+NO_2 respectively, give an estimate of the ϱSi/PN uptake ratio. This ΔSi/ΔN ratio varied between 2.3 mol mol^{-1} in October-December 1992 and 4.2 mol mol^{-1} in October 1993-February 1994. Interestingly, during *KEOPS* ϱSi/ϱPN uptake ratio averaged 4.9 ± 1.0 mol mol^{-1} at the HNLC reference station and Mosseri *et al*. (2008) reported the occurrence of strongly silicified diatoms, actively growing on ammonium (39-77% of the total N uptake). The community structure of the diatom assemblage of the *KEOPS* HNLC reference station was also close to that reported for KERFIX by Fiala *et al*. (1998) with a predominance of the genus *Fragilariopsis* Hustedt *in* Schmidt, 1913 including *Fragilariopsis pseudonana* (Hasle) Hasle 1993 and *Fragilariopsis kerguelensis* (O'Meara) Hustedt 1952 (Armand *et al*., 2008a; Quéguiner *et al*., this volume). During *KEOPS* the Plateau stations (iron-enriched waters) showed much lower, albeit more typical, ϱSi/ϱN uptake ratio averaging 1.6 ± 0.5. The KERFIX dataset is thus consistent with the *KEOPS* dataset. Both support the idea that iron-limited diatoms (Blain *et al*., 2007) growing in the well-mixed layer of the HNLC system, off Kerguelen Islands, encounter unfavorable conditions for H_4SiO_4 uptake and growth. However, despite their inefficiency in H_4SiO_4 uptake, owing to very

low growth rates, Antarctic diatoms build strongly silicified frustules which certainly play an important role in their life strategies by preventing their predation by grazers.

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